

XXI. ON A NEW SPECIES OF BRANCHIO-
DRILUS AND CERTAIN OTHER AQUATIC
OLIGOCHAETA, WITH REMARKS ON
CEPHALIZATION IN THE NAIDIDAE.

By J. STEPHENSON, M.B., D.Sc. (Lond.), Major, I.M.S.,
Professor of Biology, Government College, Lahore.

(Plates xi—xii.)

I received in November 1911 a tube of small aquatic Oligochaeta, sent to the Indian Museum from Madras by Prof. K. Ramunni Menon. The tube contained eight specimens, of which however one was a fragment incomplete at both ends. In one case the animal was in process of dividing asexually; none possessed sexual organs.

The worm belongs to the group of gilled Oligochaetes, and is closely related to the two Naids described, one by Bourne (4) under the name of *Chaetobranchus semperi* from Madras, and one by myself (15) as *Lahoria hortensis* from Lahore. Since gilled Oligochaeta are interesting on account of their rarity, and since the present form gives occasion for some remarks on the "cephalization" of the Naididae, I describe it here as far as possible in detail. My remarks go under four heads:—(1) Anatomy, (2) Asexual reproduction, (3) Systematic position, (4) Cephalization in the Naididae. It is to be remembered that I have only had the opportunity of examining preserved specimens.

(1) Anatomy.

In length the worms were from 8 to 15 mm.; they were brownish in colour; the two longest consisted each of 130 segments, plus a number of minute and scarcely differentiated segments in process of formation at the posterior end; another specimen had 77 segments with again a similar region of newly forming segments posteriorly. The gills were in most specimens just visible to the naked eye as processes on the anterior portion of the body. The prostomium was short and rounded. Succeeding the mouth was a short prebranchial region, which will be considered more fully below.

Gills.—The gills are elongated hollow evaginations of the body-wall; as in the related forms mentioned above, they contain a vascular loop, and, in the anterior portion of the body, the capillary dorsal setae also. Since they correspond in position with the dorsal setal bundles, they form a dorso-lateral series on each side. They diminish in size posteriorly, and the long dorsal setae are then no longer enclosed in them.

In the specimens in which the gills were best developed they were in the most anterior segments, about .54 mm. in length; but exact measurements are difficult, owing to their being somewhat curled and twisted; in the next succeeding segments, where they are longest, they were .72 mm. long, or about $2-2\frac{1}{2}$ times the diameter of the body in this region. In other specimens they were frequently not so long,—about .27 mm., or equal to the diameter of the body.

Some idea of the progressive diminution in size may be obtained from the following data:—in an animal of 130 segments, the gills at the 40th segment were small finger-like lobes, at the 50th large tubercles, at the 60th small tubercles, and beyond this absent. In another specimen of 130 segments, they disappeared at the 76th segment; in one of 87 segments, at the 67th; they were present, as tubercles only, on the 73rd and 56th segments of two animals whose posterior ends had been destroyed at these levels respectively; and in another specimen they were quite small finger-like lobes on the 17th, and disappeared altogether beyond the 24th segment. Behind the region of the gills, in these preserved specimens, the series is continued as a pushing out of the body-wall, which is raised round the base of the dorsal setal bundles into small pointed conical elevations; but these are merely such as would be produced by a contraction of the muscles of the setal sac pushing out the bundles of setae, and indeed may have been so produced at the moment of fixation.

Pigmentation.—As in the related forms the anterior end of the body is markedly pigmented (pl. xi, figs. 1, 2, 3). The pigment occurs as irregular blotches on the prostomium and pre-branchial region; behind this it has a fairly definite segmental arrangement, as irregular bands extending over the dorsal and lateral surfaces, but leaving the ventral surface free; the bands are formed of a number of irregular spots or blotches, which may or may not be confluent. The pigment may be very slight in amount and scattered in its distribution; in any case it fades away after the first few segments, e.g., beyond the 8th, 12th, or 13th.

Pigment also usually, but not always, occurs on the gills,—not all over them, but in streaks along their lateral aspects (pl. xi, fig. 1). The pigmentation of the gills corresponds roughly, as regards number of segments, to that of the body.

The pigment appears to be located in peritoneal cells lining the body-wall, and to be of the same nature as that of the chloragogen cells; similar cells invest the dorsal vessel as far forward as the second gill, and sometimes some of the lateral loops also [v. *inf.*, and cf. Bourne (4), and his fig. 3].

Setae.—The dorsal setal bundles begin with the gills; the setae are of two kinds, long and short. The long ('capillary') are straight, smooth, tapering gradually to a very fine point, and, where they are free from the gills and can be measured, in length commonly about 330 μ . The shorter ('needle') setae have typically the form shown in fig. 1; the distal curve and the

extremely slender extremity are (in preserved specimens) with difficulty visible with the ordinary high power, and an immersion lens is necessary to appreciate them. These setae are about 100μ long, and are closely applied to the proximal part of the shaft of the longer seta, the distal curved end of the short seta appearing to fit round the shaft of the longer. The point of the short seta may project slightly above the surface of the body in the middle and posterior regions of the animal's length.

In the most anterior part of the body, where the gills are longest, the setae are entirely enclosed in the gill processes. Here each bundle consists of two hair setae, or sometimes of only one; if there are two, one is much longer than the other. The hair setae are here much slenderer than they are posteriorly. This is the condition in the first 12, 13, 18, 26 or 27 gilled segments.

In the next succeeding region of the body the gills are becoming shorter, and the hair setae project freely and are no



FIG. 1.—*Branchiodrilus menoni*: dorsal needle-seta; \times about 375.

longer contained in the gills. The bundles are composed of one hair and one needle. The transition from a thin to a thick type of hair seta is marked, and quite sudden. The needle has apparently not the typical shape described above; it is straighter, almost or quite without the distal curve, but it narrows rapidly to a fine point, like the curved form.

In the middle and posterior regions of the body the dorsal bundles consist of one hair and one needle, of the typical forms described above. Occasionally two needles occur in a bundle.

The ventral setae of the branchial and posterior regions of the body may be separated into two forms, though the distinction is not a hard and fast one, since intermediate shapes occur; neither is the distribution of the two forms fixed.

The one form, the more numerous, which may be designated the 'posterior,' is distinguished by a comparatively stout shaft, often a somewhat greater length, a nodule distal to the middle of the shaft, and by having the prongs of the fork equal in length or the distal prong slightly longer (fig. 2). In length they measure

110 to 139 μ (proximal to nodulus : distal to nodulus : : 61 : 49, or 82 : 57). The other or 'anterior' type is slenderer throughout, the prongs, especially the distal prong, also longer and slenderer; the distal prong is $1\frac{1}{2}$ times as long as the proximal, while the



FIG. 2.—*Branchiodrilus menonii*; setae of the posterior ventral type; $\times 375$.

nodulus is at the middle of the shaft or somewhat proximal (fig. 3). In length they measure 100 to 116 μ (proximal to nodulus : distal to nodulus : : 57 : 57, or 55 : 61). In both types the distal prong is only about half as thick at its base as the proximal.

The 'anterior' type occurs on a comparatively small number



FIG. 3.—*Branchiodrilus menonii*; setae of the anterior ventral type; $\times 375$.

of the anterior segments of the body, the posterior type on the remainder; but there is no defined limit to their distribution. Thus well-marked 'anterior' setae may be found on segment xiv, and even behind this; or nearly all the ventral setae in the body may be of the 'posterior' type. The change from 'anterior' to 'posterior' is in any case not a sudden one, and may apparently

take place at a different level on the two sides of the same animal.

As to the number of ventral setae per bundle, this is usually three, and I have never seen more except in the one instance shown in pl. xi, fig. 4, where one of the bundles has four. Posteriorly there may be only two; and in some of the anterior segments also there may only be two. Very commonly in the anterior segments there were two fully formed setae, along with a half-formed seta, of which the proximal end was wanting,—as if it were still in process of formation, or perhaps rather as if its formation had been permanently arrested at this stage (cf. pl. xi, fig. 4).

Prebranchial region.—The region between the first gill and the mouth is in this species peculiar in several respects, and seems to merit special description. It may be recalled that in Bourne's worm dorsal and ventral setae begin at the same level (segment ii), the interval between mouth and first setae being equal, according to his figure, to about a single body segment; cephalization is therefore limited to the first segment. In the allied worm previously described by me there is a considerable interval between mouth and first gills; in this interval are situated the four first ventral setal bundles (exceptionally only three) but no dorsal setae; the gills and dorsal setae, therefore, begin on the sixth segment, and the first five segments are 'cephalized.'

In the specimens now under discussion, there is a moderate interval between the mouth and the level of the first gill, equal on the average (cf. pl. xi, figs. 1, 2 and 3) to the diameter of the body at the latter situation. No distinct external annulation could be made out in this interval; and the pigmentation was not segmentally arranged. The most curious point however is the varying distribution of ventral setae in this region.

The setae are always, when present, of a type distinct from those in the rest of the body. In their general proportions they resemble the 'anterior' setae, but are considerably shorter (77 to 87 μ), remarkably slender, with delicate prongs, and a nodulus proximal to the middle of the shaft (proximal : distal :: 36 : 41, or 41 : 46).

Their distribution was as follows. In one specimen (pl. xi, fig. 1) there were four bundles of such setae in the prebranchial region; in another three (pl. xi, fig. 2); the condition in these specimens (except for the small size of the prebranchial setae) was therefore the same as in the related species previously described by me. In a third specimen there were on one side two setal bundles, of only one seta each, the anterior of the two being the longer; on the other side there was, near the mouth, a single bundle of two setae; the prostomium in this specimen was fairly well formed, and the prebranchial region of considerable extent; i.e. considering the manner in which asexual division takes place in this form (v. *inf.*), this specimen had probably been leading a free existence for some time. In a fourth there was on one side a single bundle, of one seta only, situated nearer to the first gill than to the

mouth; on the other side there were no setae; the prostomium was very round, and the impression given was that the animal had not been long separated. A fifth specimen had no prebranchial setae on either side; the prostomium was very well marked, the mouth and the structures of the head in general were well formed; moreover this was the specimen in which asexual division was going on at the posterior end (pl. xi, fig. 4); it seems justifiable to suppose that this animal had been leading an independent existence for some time. A sixth specimen had similarly no prebranchial setae on either side; the setae of the first gilled segment were smaller and thinner than those of succeeding segments; the differentiation of the head end of the animal was however incomplete, the shape, and the relations of mouth and pharynx did not appear normal, and the gills ceased, even as tubercles, after the twenty-first segment; it seems not improbable, therefore, that this animal had only recently been separated, and had still to undergo a certain amount of development at this anterior end. The seventh specimen had no prebranchial setae, and setae were also absent on the first gill-bearing segment (pl. xi, fig. 3); the prostomium, mouth, pharynx and cerebral ganglion were well formed, and the animal had probably therefore been separated for a considerable time.

It is perhaps worthy of remark that in the fifth and seventh of the above specimens the prebranchial region seemed to present a somewhat indefinite, thicker or denser appearance of the tissues and a consequent slight opacity, as compared with the segments behind it. Whether this is of any importance or not is perhaps doubtful; but it reminded me of a similar somewhat denser and more opaque appearance of the tissues which is seen at the hinder end, in any of the Naididae, in the region where new segments are forming but not yet differentiated.

It is evident, in any case, that the distribution of setae in the anterior part of the body varies very considerably. So far as I am aware, such marked variations have not been noticed in any other form. Further remarks on the import of this variability will be found below.

Other anatomical features.—In sections through the middle of the body, the sides of the animal are seen, in these specimens, to be somewhat pinched in; and at the level of each septum a distinct band of muscular fibres passes on each side from the lateral line to the gut; it is presumably the contraction of these fibres that causes the constriction referred to.

The pigment cells, as seen in sections, are large irregular cells, containing a large number of brown granules, and indeed appearing to be made up of them (pl. xi, figs. 5, 6). The cells occur in several situations,—(a) round the dorsal vessel and lateral commissures, (b) along the muscular fibres passing through the coelom from gut to parietes, (c) inside the muscular layer of the body-wall, (d) apparently more or less free, as corpuscles inside the body-cavity, attached however to the inner surface of the parietes by processes of the pigment cells themselves, or of other corpuscles.

The buccal cavity is tubular, and is succeeded by the pharynx, a portion of the tube which possesses a strongly ciliated and laterally extended dorsal diverticulum, the cells lining which are markedly columnar; while the ventral wall of the pharynx is composed of flatter and more irregular cells (pl. xi, fig. 5). The pharynx extends backwards to include the first gilled segment; the diverticulum then flattens out and disappears. The oesophagus is strongly ciliated; there is no stomach,—indeed, beyond the pharynx, the tube can scarcely be differentiated into distinct regions.

The dorsal vessel is, for by far the greater part of its extent, dorsal in name only; it runs for the most part on the left of the intestine (pl. xi, figs. 2, 6); it is invested by chloragogen cells and pigment cells as far forward as the interval between first and second gills; here it becomes dorsal, and loses its investment.

The present species does not stand alone in the matter of the aberrant course of the dorsal vessel. I have ascertained, from an examination of my specimens, that *B. hortensis* is similar in this respect, though the fact was not noted in my original account of this worm. It is known also to be the case in the various species of the genus *Dero* (Naididae), and in *Branchiura sowerbyi* (Tubificidae) (1, 13); and I have found it also in the Tubificid worm I have described (13) as *Limnodrilus socialis*. One peculiarity common to all these forms is that they possess specialized respiratory arrangements;—*Dero*, *Branchiura*, and *Branchiodrilus* possess branchiae, while *Limnodrilus socialis* has a well-developed integumentary blood plexus in the posterior part of its body, and during life is incessantly waving this posterior end in the water; but as to what connection there is between such specialized respiratory arrangements and a lateral or ventrolateral position of the dorsal vessel I am not clear.

There is a large giant fibre on the dorsal surface of the ventral cord, looking in sections like a large empty tube (pl. xi, fig. 6).

(2) *Asexual Reproduction.*

One specimen only was dividing asexually (pl. xi, fig. 4); and here a fragment only of the posterior animal was present. The whole specimen consists of 87 segments in the anterior animal, and nine segments of the posterior. Though apparently nearly ready for detachment, there is as yet no differentiation of a head in the hinder zooid, no mouth, and no new setae, no newly formed segments, nor any region intervening between the first gilled segment and the anterior end of the body; the gills however have formed, and the characteristic pigmentation of the anterior region is beginning to appear. At the posterior end of the anterior animal there is an appearance suggestive of the approaching rapid formation of a budding zone,—a slight opacity, and an irregular fine transverse streaking, more especially on the ventral half of the body.

The condition is therefore to be compared with what occurs in Bourne's *Chaetobranchus*, where there is no budding zone, and the process of division resembles rather a simple fission of the animal into two. It is to be contrasted in this respect with the species I found at Lahore, where a regular budding zone is formed, as in *Nais*, *Chaetogaster*, etc. Further, the present form agrees with Bourne's in the fact that asexual reproduction is apparently a comparatively rare occurrence; Bourne, out of a large number, found only a few specimens dividing; whereas in many species of Naididae it seems to be rather the exception than the rule to find an animal which is not preparing to divide.

It would appear from the specimen undergoing division (pl. xi, fig. 4),—if I am right in supposing that a separation of the two individuals was here not far off,—that a considerable amount of the development of the head has still to be gone through after fission is completed. This is confirmed by the actual condition of two of the free-living specimens examined (the fourth and sixth; cf. *ant.*, under the description of the prebranchial region).

Can this inference be used to explain the remarkable variations in the distribution of the prebranchial setae? In other words, can we suppose that all specimens which show fewer than four pairs of ventral setal bundles in front of the gills have recently been separated, and have not yet completed the development of the anterior end,—and that the production of the full number of setal bundles will follow in time? Would the specimens described above have developed, in all cases, four bundles of ventral setae in the prebranchial region if they had been left alive?

This seems quite possible with regard to such specimens as the fourth and sixth of the foregoing description; here the other structures of the anterior end—prostomium etc.—were also incomplete, and it is quite possible that the setae might, later, have developed along with these.

It does not seem very probable with regard to some of the other specimens. For example, in that represented in pl. xi, fig. 3, the seventh of the previous description, the prostomium, mouth, and other features of the anterior end are well developed, yet the ventral setae are wanting; had they been going to develop, there would have been at least some signs of them. The same may be said with regard to the fifth. And in the specimen with three well-developed setal bundles in the prebranchial region (pl. xi, fig. 2) there would probably have been some sign of a fourth if a fourth had ever been going to develop. Again, asexual reproduction apparently here, as in Bourne's worm, does not occur with any great frequency; hence the chances are very much against six out of these seven specimens having been very recently separated, as the above explanation would demand.

The matter may therefore be summed up as follows:—In the present form the process of asexual reproduction is accompanied by the formation of only the rudiment of a budding zone; separation of the two resulting individuals takes place early;

and a considerable portion of the process of differentiation of the head is completed after separation. In this differentiation, the formation of the setal bundles sometimes lags behind that of the other structures, and the number of setal bundles formed varies considerably. Not infrequently, it would appear, none are formed; and the maximum number of four is perhaps comparatively seldom produced.

(3) *Systematic Position.*

Though closely related to the worm which I have described as *Lahoria hortensis*, the present species is not identical with it; and the more restricted distribution of the gills in the form under discussion, the details of asexual reproduction, certain differences in the form of the setae, and the smaller number of these in both dorsal and ventral bundles, are sufficient to distinguish it.

With regard to Bourne's *Chaetobranchnus semperi* the agreement is in many respects closer. Thus Bourne gives identically the same number of segments (130) which I counted in the best developed specimens of the present batch; the details of pigmentation correspond in the two; the number and distribution of the gills is about the same; the details of asexual reproduction are strikingly similar, and different from what is usual in other Naididae; and finally both were taken in the same locality.

On the other hand there are several points of difference. To begin with the less important, the length of Bourne's worm appears to have been greater, though some of the apparent difference is no doubt due to contraction of the preserved specimens; the setae did not begin to project freely so soon in Bourne's specimens (about the 30th segment), as in mine (13th to 28th); and, to judge from Bourne's figure, the position of the mouth is different in the two, the prostomium being considerably longer, and the prebranchial region somewhat shorter in Bourne's specimens than in those now under discussion. Further and more important differences are found in the characters of the setae; though those of the two forms have a general resemblance, this does not extend to details (compare, for example, the dorsal needles of the present form with the sickle-shaped dorsal setae of *Chaetobranchnus semperi*); and a marked distinction is found in the numbers of setae per bundle, both in the dorsal and ventral series. Lastly there is the fact that in the present form there may be as many as four pairs of ventral setal bundles between the first gills and the mouth.

In my present specimens, it is only in a minority that well-formed setal bundles are developed between the first gills and the mouth; and had I received a smaller number of the worms, say two or three only, it is not improbable that such examples would have been wanting altogether; in which case, in view of the many and detailed points of similarity, it is not unlikely that I should have recorded the present find as a rediscovery

of Bourne's worm. It does not seem possible, on the other hand, that Bourne should have overlooked the occasional occurrence of prebranchial ventral setae, since he "secured numerous specimens of *Chaetobranchus*" and (with regard to the mode of asexual reproduction at least) "examined a very large number of individuals."

The two forms are therefore to be regarded as distinct, and I accordingly propose for the one herein described the specific name *menoni*. It seems however impossible, merely on the ground of a (far from constant) difference with regard to the prebranchial setae, to deny a close genetic relationship between the two. They must undoubtedly be regarded as belonging to the same genus.

For the generic name *Chaetobranchus*, which, since it is the name which Bourne used, has been employed above in referring to the worm described by him, Michaelsen (8) substituted *Branchiodrilus*, *Chaetobranchus* having been previously used for a fish. The new worm thus becomes *Branchiodrilus menoni*.

If however these two species are ranked under the same genus, so must be the form from Lahore described by me as *Lahoria hortensis* (15); since the reason for separating this latter as a distinct genus from Bourne's worm was the same difference with regard to the prebranchial setae which occurs or may occur in *B. menoni*; i.e. the fact that four (or three) pairs of ventral setal bundles may occur in front of the first gills, or rather (which comes to the same thing) in front of the first dorsal setae.

The genus therefore now comprises three species, and genus and species will be defined as follows:—

BRACHIODRILUS Mchlsn. (= *Chaetobranchus*—Bourne):

Prostomium rounded. A pair of dorso-laterally placed branchial processes on many or most of the body-segments, beginning immediately or a short distance behind the mouth. Ventral setae crotchet shaped, forked distally. Dorsal setae beginning in the same segment as the gills, of two kinds, capillary and needles; the former, in a number of the anterior segments, enclosed in the gills.

1. *B. semperi* (Bourne).

Length 38-50 mm., diam. .5 mm., segments 130. Branchial processes begin in the segment behind the mouth; at first are about four times as long as the diameter of the body, then decreasing in length and disappearing at the 60th—70th segment. Dorsal setal bundles consist of two or three capillary setae, longer in the anterior, shorter in the posterior segments, and two or three short sickle-shaped setae, the latter wanting in the anterior segments. Capillary setae of dorsal bundles all enclosed in the branchial processes in about the first 30 segments, some so enclosed in about the next 30, thenceforward all free. Ventral

bundles of 4-6 setae, the distal prong of which is the longer in the most anterior segments, the proximal being the longer in the remaining segments. No stomach. Lymph corpuscles rounded, with numerous olive-green granules. Asexual reproduction without the previous formation of a budding zone.

2. **B. menoni** sp. nov.

Length (preserved) 8-15 mm., segments up to 130. A short prebranchial region between first gills and mouth, which may or may not possess a series of pairs of ventral setal bundles (up to 4 pairs). Gills diminishing in size posteriorly, and ending some distance in front of hinder end; longest gills $2\frac{1}{2}$ times as long as diameter of body. Dorsal setal bundles anteriorly of one or two hair setae; in the middle and posterior parts of the body of one hair and one needle seta, the latter somewhat bayonet-shaped, tapering to a fine point. The hair setae of the anterior bundles enclosed in the gills; becoming free before the 30th segment. Ventral bundles usually of 3, sometimes of 2, setae; anteriorly slenderer, distal prong longer, nodulus proximal to middle of shaft or about its centre; further back the setae are stouter, distal prong approximately equal to or a little longer than proximal, nodulus distal to middle. No stomach. Asexual reproduction without or almost without previous formation of a budding zone.

3. **B. hortensis** (Stephenson) (= *Lahoria hortensis*).

Length 16-25 mm., diam. .5-.75 mm., segments 90-120. Gills and dorsal setae begin on sixth (occasionally fifth) segment. Gills diminishing in size posteriorly, ending just in front of hinder end of animal; longest gills 3-4 times as long as diameter of body. Dorsal setal bundles of capillary and needle setae, not more than two of each per bundle; contained within the gills for the first 40-50 segments, then one hair seta of each bundle free; needle setae straight, pointed. Ventral bundles of 4-5 setae, distal prong slightly longer than proximal, and much thinner at its base. No stomach. A budding zone formed during asexual division.

4. *On Cephalization in the Naididae.*

Cephalization means the formation of a head; to quote from Beddard (2), "Lankester has applied this expression to the specialization of the anterior region of the body so frequently seen among the Oligochaeta." This specialization shows itself perhaps most prominently in the distribution of the setae;—"all Oligochaeta show cephalization as regards the first segment of the body, which never possesses setae." The Naididae which (except *Chaetogaster*) have regularly ventral setae in all segments from the second onwards, frequently lack dorsal setae in a number of the anterior segments, and there are thus in these cases

a number (usually four, i.e. segments ii—v) of segments which have ventral but no dorsal setae. It is frequently found moreover, e.g. in the genus *Nais*, that the ventral setae of these 'cephalized' segments are different in type from the succeeding ones: thus the distal of the two prongs of the forked end may be relatively longer, and the nodulus situated proximal, instead of distal, to the middle of the shaft.

Other systems or organs are concerned. Beddard instances septa and nephridia, which may be absent from the anterior segments. In addition I may adduce pigmentation; the cephalized segments may be lighter in colour, or the pigment may be differently arranged, as compared with the following segments. Chloragogen cells are absent from the alimentary tract in the cephalized segments. The gills of *Branchiodrilus hortensis* are similarly absent from this region.

The next point which I wish to bring forward is that this cephalization is related in the Naididae to the manner of asexual division, and to the production, between two separating individuals, of a budding zone. When one of the Naididae divides asexually, the usual procedure is that at some spot near the middle of the length of the animal a rapid production of new segments takes place; of these segments the larger number go to form the tail end of the anterior, the smaller number to form the head of the posterior, of the two resulting animals. This head commonly consists of five segments, with a prostomium, all newly formed; i.e., it corresponds to the number of cephalized segments as determined by the examination of free-living specimens. In other words these segments, produced in the budding zone, and representing the head of the (subsequently to be detached) animal, want the dorsal setae, and frequently have the ventral setae modified; they are commonly, at first at least, less pigmented (as are also the newly formed segments at the posterior end of the anterior animal); they contain no chloragogen cells, have no nephridia, and in *Branchiodrilus hortensis* are without gills.

Since the predominant mode of reproduction in the Naididae is the asexual, by fission,—sexual reproduction being a comparatively, or absolutely, rare occurrence,—by far the larger number of individuals of a species existing at any time will have been produced asexually, and *the cephalized segments will be those which have been produced in a zone of budding.*¹

¹ This point with regard to the budding zone has not apparently received much attention from students of the Naididae and (in the somewhat scanty literature at my disposal) I cannot find any references as to how many of the segments produced in the budding zone go to the anterior end of the posterior animal in the different genera. My own observations on the genera *Chaetogaster*, *Nais*, *Slavina*, *Stylaria*, *Aulophorus* and *Branchiodrilus* show that the rule just stated holds for these (in *Chaetogaster*, where there are no dorsal setae, cephalization is marked by the regular series of ventral setae beginning only in the sixth segment); and it apparently holds also for *Aeolosoma* (fam. *Aeolosomatidae*), where the process is similar. It is to be noted however that *Pristina* is a remarkable exception: here no fewer than seven of the anterior segments are formed in the budding zone, though dorsal setae begin on the second segment, and cephalization is therefore confined to the first.

From this it follows, that variations or irregularities in the process of budding will give rise to corresponding variations or irregularities in the degree and form of cephalization.

That the budding zone varies in position has been known for some time. It is usual, following Bourne (5), to denote by n the number of segments of the original animal behind which the budding zone appears, and though Bourne thought at first that n would be found to be constant for each species, it now appears that in a large number of species at least it varies within somewhat wide limits (for examples, cf. Benham (3), Piguet (11), Stephenson (16) (*Stylaria lacustris*)).¹

Variations in position of the budding zone would not necessarily affect the number of cephalized segments; the point has been mentioned, because variations in one respect prepare us to look for variations in other respects. Such have been noted in *Nais communis* by Piguet (11):—"à diverses reprises, j'ai trouvé un certain nombre d'exemplaires qui n'avaient que 4 segments avant celui où débutent les soies dorsales et les cellules chlorogènes (normalement, le 6me). J'ai d'abord pensé à une régénération incomplète après mutilation; mais tous ces individus avaient la région antérieure absolument normale, sauf que leur 5me segment était l'homologue du 6me des autres. Il faut donc supposer que le bourgeonnement produit quelquefois, accidentellement peut-être, des spécimens ayant, dans la région du pharynx et de l'oesophage, un segment de moins que les autres." The fact that in *Branchiodrilus hortensis* there may be either four or five cephalized segments (15) belongs here also. And in *Slavina punjabensis* I found (14) a number of irregularities in the results of the budding process;—incomplete differentiation of the head, an eye wanting on one side, fewer setal bundles, and these containing fewer setae than normal;—which might perhaps be partly explained by supposing that separation of the two individuals had taken place before the differentiation of the head had been completed, and that this differentiation would follow after, instead of as usual coming before, the separation. But it is perhaps equally likely that these irregularities were destined to endure.

This brings us to the condition in *B. menoni*. We have here before us a number of variations in the characters of the anterior end of the animal, especially in the numbers of the ventral setal bundles in front of the gills (or of the first dorsal setae). As to how this is related to the process of asexual reproduction, and how far these variations may be due merely to a delayed differentiation of the newly formed head, see the section on Asexual Reproduction. Referring to the discussion there for support, it will be sufficient now to state that in *B. menoni* we have a species which varies within wide limits in regard to cephalization, as manifested especially in the setal distribution.

¹ In the Aeolosomatidae however and in the genus *Chaetogaster*, in which cases the number of body segments is small, n would seem to be fixed for each species, according to observations on all the species that have come under my notice.

The importance of a right estimate of the value of cephalization, as marked by the want of correspondence in the anterior limits of the dorsal and ventral setae, is apparent when we call to mind that this is one of the characters by which the genera of the Naididae are discriminated. Thus the segment on which the dorsal setae begin (reckoning the first segment with ventral setae as the second of the animal's body) figures as a diagnostic mark of genera in Vejdovsky (17, p. 25), and in Michaelsen (8, p. 17). The extent anteriorly of the dorsal setae is the chief, if not the only, distinction between the genera *Naidium* and *Nais*. To quote from a former paper (15):—"Beddard (2, p. 281), merging together a number of genera of other authors under the one name *Nais*, does so largely because they 'agree in the important fact that the first five segments are cephalized,—that the dorsal setae do not commence until the sixth segment,' and by implication would exclude from the genus any form which did not show this cephalization. Similarly *Pristina* and *Naidium* are united by him on the ground of the absence of this feature. Bourne (5) also believed that the number of cephalized segments is constant for the genus, and thought it probable that *Dero furcata*, possessing four achaetous dorsal segments, should on this account be removed from the genus, since the other members of it have five such segments." And specially with regard to *Branchiodrilus*, "the presence of dorsal setae on all segments from the second onwards is mentioned as a feature in the generic diagnosis of *Branchiodrilus* in Bourne's original paper (4), in Beddard's monograph of the Oligochaeta (2), and by Michaelsen (8)."

It is therefore evident that a distinction such as that which obtains between *Branchiodrilus semperi* and *B. hortensis*, where the dorsal setae begin on the second and sixth segments respectively, is held by most authorities as a ground for a generic separation. Holding this view myself, I accordingly separated the Lahore species as a distinct genus, *Lahoria*, though I thought it "perhaps worth while asking whether a cephalization which affects only the setal distribution (for the absence of gills on segments ii—v of the present form [i.e. *B. hortensis*] is evidently correlated with the absence of the setae which are necessary to stiffen them) has the systematic value hitherto generally attributed to it."

It is to be added that the above view, of the absolute value of a different anterior extent of the dorsal setae as a generic character, has not always been strictly maintained. Thus Michaelsen (8) unites into one genus *Paranais* three species known at various times as *Naidium naidina*, *Paranais littoralis*, and *Uncinais uncinata*, though their dorsal setae begin respectively on the second, fifth, and sixth segments. And in a recent paper (9) the same author prefers to include my *Lahoria hortensis* as a species of *Branchiodrilus* (as I do in the present paper), allowing the numerous close structural resemblances to over-ride the somewhat artificial distinction based on the distribution of the dorsal setae.

With the discovery of *B. mcnoni* the case becomes stronger. I was in doubt at first as to whether it would not be advisable to unite it with Bourne's worm under the same species, *B. semperi*; since the points of structural agreement are many, and in some cases extend into detail; and there can at least be little doubt of a close genetic connection. Yet, allowing the usual value to cephalization, the difference between some specimens of *B. mcnoni* and *B. semperi* would be generic; and indeed the same might be said of specimens of *B. mcnoni* alone, when compared one with another.

The conclusion to be drawn is that *the degree of cephalization in the Naididae is correlated with the behaviour of the segments of the budding zone,¹ and that variations in both, of considerable extent, may occur within the same species. The form of cephalization which is characterized by the absence of dorsal setae from a number of the anterior segments of the body has been evolved repeatedly, in different groups of the Naididae, and at different times. The degree of cephalization is not necessarily a generic character, since differing degrees of cephalization may coexist with a remarkable similarity in general organization.*

One point of a more speculative nature remains. In the case of *Branchiodrilus hortensis*, which usually has five prebranchial segments, specimens are occasionally met with which possess only four such segments; in these cases the first gilled segment would seem to be homologous throughout, i.e. the sixth segment of some individuals is homologous with the fifth of others. Similarly, according to Piguet, in *Nais communis* (v. ant.):—"mais tous ces individus (i.e. those with only four segments in front of that on which the dorsal setae began) avaient la région antérieure absolument normale, sauf que leur 5me segment était l'homologue du 6me des autres."

Similar considerations must be extended to *Branchiodrilus mcnoni*; the first gilled segment is homologous, throughout the individuals of the species, though these individuals vary as regards the number of segments intercalated in front of this fixed point and behind the mouth.

But while some specimens of *B. mcnoni* agree in the arrangement of their segments (as determined by the setal bundles) with *B. semperi*, others agree with *B. hortensis*. It follows that the first gilled segment is homologous in these two species, i.e. segment vi of *B. hortensis* is homologous with segment ii of *B. semperi*.

If this is the case, then we must infer that the same holds generally in the Naididae, and that the segment immediately succeeding those produced in the budding zone,—usually, but not always, that on which the dorsal setae begin,—is homologous throughout the group.

¹ Compare however what was said previously (footnote p. 230) regarding *Pristina*.

As to whether this would lead to difficulties with regard to the homologies of the genital organs or not I cannot say. It would be interesting to have details of the budding process and of the position of the genital organs in *Naidium*, where the dorsal setae begin on the second segment; but these are lacking. The above views would not lead to any difficulties in the case of *Pristina*; here the testes are in segment vii, the ovaries in viii, i.e. the genital organs are displaced two segments backwards as compared with other genera. But the segments contributed to the animal's head from the budding zone are also more numerous than usual, seven instead of five, and therefore the testes are still in the last segment to be added from the budding zone, as in *Nais* and other genera.

II.

Branchiura sowerbyi, Bedd.

This interesting worm, belonging to that small group of Oligochaeta which possess gills, was first described by Beddard (1) in 1892 from specimens obtained from the mud of the *Victoria regia* tank in the Royal Botanical Society's Gardens in London; of these specimens only one was sexually mature, and this furnished the material for his description of the genital organs. No more was heard of this worm till 1908, when Michaelsen (7) found specimens, among them several sexually mature, in a warm water tank of the Botanical Gardens at Hamburg; Michaelsen's account deals exclusively with the genital system, in which he finds a number of differences as compared with Beddard's description. L. Perrier (10) shortly afterwards notified the discovery of numerous specimens in the Rhone, but did not add any anatomical details. Lastly in 1911 I (13) found the worm in a nullah near Lahore in the Punjab; I was able to add a number of anatomical facts to those recorded by Beddard, but none of my specimens were sexually mature.

I have since then received specimens from two sources. In May 1911 Mr. Gravely of the Indian Museum sent me a tube containing living specimens of the worm taken in Calcutta; they were obtained from mud in an earthenware basin containing aquatic plants planted in mud and water in the Museum garden. It is noteworthy that the worms were put into the tube on the 12th May, and were received by post in Lahore at 4.30 p.m. on the evening of the 15th; the tube was opened immediately, and the worms were found to be still quite lively. The mean temperature at Lahore for the 24 hours was at this date 90°, the maximum in the shade 106°F, and the temperatures must certainly have been higher in a railway van coming from the south.

A few observations were made on the movements of the living worm. As remarked above, they were quite active. The posterior part of the body was at times held quite still while the

anterior part was wriggling; the movements of the posterior part, when these occurred, were either irregular wriggings or regular undulating movements. The gills in these specimens showed no movements of their own when the tail was at rest. The worms manifested a sharp and sudden response to a touch with a needle; they contracted somewhat, and then as a rule remained quite motionless for a short time, subsequently resuming their movements.

As to their external characters, the gill region was short; in one case well developed gills ceased suddenly a little distance in front of the hinder end, and behind this point there were only tubercles,—about a dozen in both dorsal and ventral series, the two or three most posterior being slightly larger than the rest; this peculiarity was possibly due to previous injury. On holding the tube up to the light and looking through it the gills were invisible to the naked eye in the living animal on account of their transparency; their length was not greater than the diameter of the body. The length of the animals was from $1\frac{3}{4}$ to 2 inches when extended, and their breadth 1 mm. or more. One specimen exhibited genital organs, as described below.

Again in November 1911 I received from the Indian Museum a tube of these worms, preserved, which had been taken in Madras, in the mud from the *Victoria regia* tank in the Agrihorticultural Society's gardens, in September-October, 1907, by Prof. K. Ramunni Menon. The specimens were in a bad state of preservation, and consisted of 18 fragments, of sizes from 25 to 2 mm., mostly small; these had apparently belonged originally to two worms, of which neither showed sexual organs. The peculiarity about these specimens was that they were constricted, in transverse section, so as to show a somewhat figure-of-eight appearance; but the dorsal, and still more the ventral, surface was flattened, the ventral surface, in the region in front of the gills, giving the appearance of a flat sole.

The occurrence of a sexual specimen among the worms received from Calcutta offers the opportunity of adding a few remarks on the genital organs. The differences between the descriptions given by Beddard and by Michaelsen are very considerable. As briefly as possible, the chief of these are as follows:—Michaelsen finds that the vas deferens enters the proximal expanded portion of the atrium very obliquely through the wall of the latter, nearly but not quite at its rounded extremity; this portion of the atrium is lined by long columnar epithelium, surrounded by a voluminous investment of glandular cells, and encroaches posteriorly, where the vas deferens joins it, on segment xii. It merges anteriorly into the middle region of the atrium, which is narrower, undergoes several irregular windings, and before becoming the distal region of the atrium is joined by the paratrium. The distal region of the atrium is again wider, is bent at its upper end like a hook, but its main portion passes vertically downwards to the male aperture. The paratrium is a long

diverticulum from the middle region of the atrium, closely bound up with the atrium for some distance near its origin, then separating from it though still running parallel; it extends back through the whole extent of segment xii, has an insignificant lumen, and is, like the proximal portion of the atrium, covered with a thick layer of glandular cells. A special ovoid coelomic sac encloses the distal section of the atrium and so much of its middle section and of the paratrium as are bound up together. The spermathecae consist of a duct with an expanded spherical ampulla.

Beddard on the other hand shows the vas deferens as joining the atrium about the middle of the length of the latter. The internal half of the atrium has thus the appearance of being a diverticulum of the male efferent canal; it is a large ovoid sac, with a considerable lumen and a voluminous investment of gland cells of peritoneal origin. The distal half of the atrium, below the junction of the vas deferens, is tubular, and is surrounded by a considerable muscular investment. The spermathecae are pear-shaped.

The differences briefly indicated above might possibly be explained, according to Michaelsen, in one or more of three ways. First, Beddard's specimen might not have been fully mature; but this explanation is in any case not by itself sufficient, and moreover the clitellum was well developed in Beddard's specimen, and the spermathecae contained spermatozoa. Or Beddard may have been misled, owing to the scantiness of his material, and the difficulty of working out a complete description from one specimen only; in this case it may have happened that Beddard has overlooked the paratrium, and mistaken the relation of vas deferens to atrium. Lastly, the specimens of the two observers may have belonged to different species; this however Michaelsen thinks very unlikely, since if the above differences do actually exist they are not of specific but of generic importance.

The sexual specimen from Calcutta, mentioned above, was pretty certainly not fully mature; in the sections, ripe spermatozoa are indeed seen entering the seminal funnel, and the sperm sac extends as far backwards as segment xiv; but the clitellum is indistinguishable, the spermathecae contain no spermatozoa, and there is no ovisac with contained ova. But in the circumstances above mentioned, the examination of other sexual specimens of this worm is a matter of some interest and importance; and the present specimen has probably this advantage, that it will at least indicate whether the differences in the two already published accounts are or are not due to the first of Michaelsen's suppositions,—i.e. to Beddard's having worked on an immature specimen.

Briefly, the Calcutta specimen agrees with Michaelsen's description in all essential points; and a full account would therefore be quite superfluous. It will only be necessary to refer to the figures appended, and to mention the characters in which the present specimen differs from Michaelsen's account.

(i) The atrium and paratrium are confined to segment xi, and do not encroach on xii.

(ii) The proximal part of the atrium is a spherical sac, sharply marked off from the middle portion, and lined by cubical, not columnar, epithelium (pl. xii, figs. 1, 4).

(iii) There is no bulky covering of gland cells surrounding either atrium or paratrium (pl. xii, figs. 1-4).

(iv) The lower portion of the paratrium runs side by side with the middle region of the atrium in a common sheath (pl. xii, fig. 2), as in Michaelsen's specimens, but their lumina never unite, and open separately into the distal section of the atrium (pl. xii, fig. 3).

(v) The combined atrium and paratrium undergo fewer windings in the coelomic sac than is described by Michaelsen.

(vi) The distal section of the atrium is straight throughout, not hooked at its dorsal extremity (pl. xii, fig. 5).

(vii) The spermathecae are small, egg-shaped, with thick walls and small lumen.

(viii) The female efferent apparatus is not described by Michaelsen. Beddard describes an oviduct opening on the furrow between segments xi and xii. I find an ovarian funnel on septum 11/12 (pl. xii, fig. 1), which leads to the exterior by a short oviduct opening on segment xii, a little distance behind the level of septum 11/12.

I think it probable that most, if not all, the differences between the Hamburg specimens and the present one are to be referred to their being in different stages of development. And since the present specimen is presumably at a less rather than a more advanced stage of development than that described by Beddard, and since nevertheless it shows a fairly close agreement with Michaelsen's description, it does not seem likely that the discrepancies in the accounts of Beddard and Michaelsen are due to differences in the degree of maturity of their respective specimens. The explanation of those discrepancies is therefore to be sought in one of the other directions indicated by Michaelsen.

III.

Limnodrilus socialis, Stephenson.

The above worm was recently described by me (13) from Lahore, where it is common. I have twice received specimens alive from Mr. Gravely of the Indian Museum; the first occasion was in March 1911, the worms having been taken in a masonry drain at Belgatchia near Calcutta, the second in May 1911, when a tube of these worms, taken within the precincts of the Museum, was received at the same time and under the same conditions as the *Branchiura sowerbyi* previously mentioned.

Since the shape of the cerebral ganglion is largely used for purposes of discrimination and identification, I append a sketch of it, from a specimen in which it was well seen (fig. 4).

IV.

Enchytraeus indicus, sp. nov.

I received from the Indian Museum in October last a small tube of worms collected by Mr. S. P. Agharkar, of the Elphinstone College, Bombay, in the neighbourhood of that city. Mr. Agharkar's note concerning the specimens is as follows:—"Oligochaete found in egg membranes of the common pond snail *Ampullaria*. They were found in the eggs of this snail which I collected on August 18th. The eggs were kept in a moist place for hatching, and on the 6th September, 1911, the young snails came out one by one. In some of these eggs, instead of the young snail, I found this worm. In other cases however it was found in the membrane surrounding the young snail."

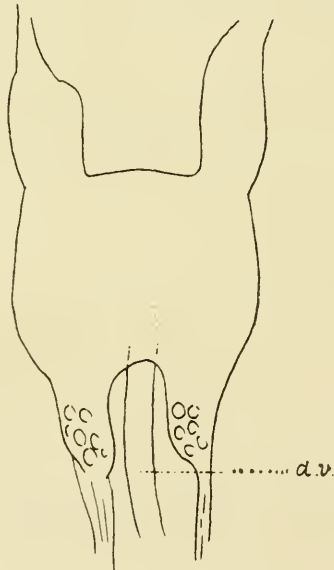


FIG. 4.—*Limnodrilus socialis*; cerebral ganglion, from above. *d.v.*, dorsal vessel.

The tube contained six specimens, of which one was very small, in a good state of preservation.

External characters.—The length was about 4 mm., the colour brownish; number of segments 31. The prostomium was short and bluntly conical; there was a head-pore between prostomium and first segment. The clitellum embraced segments xii—xiii; it was absent however from the median portion of the ventral surface of these segments.

The *setae* are of the type which is ordinarily found in the genus,—shaft straight with however a slight proximal curve, without nodulus, gently swollen towards the free extremity, and pointed at the end. In length they are approximately 50μ . The

ventral series are three per bundle in segments ii—xi, absent in xii and two per bundle behind this. The dorsal series are two per bundle throughout.

The *alimentary canal* begins in a tubular buccal cavity lined by low, approximately cubical, epithelium. The pharynx succeeds, and is in turn followed by the ciliated oesophagus, narrow as far as segment vi, a little wider in vii and viii; its calibre finally increases in xiv where the tube becomes the intestine; the cilia are specially long in segments vii—xi. Three pairs of septal glands are present, in segments iv, v and vi; their position would perhaps be more accurately described by saying that they are in close connection with septa 4/5, 5/6 and 6/7, which split to enclose them; the posterior pair of glands are united ventrally underneath the oesophagus. Peptonephridia are present as narrow coiled tubes in segment iv.

The *dorsal vessel* begins in segment xiii apparently, or at dissepiment 12/13. It divides just behind the level of the mouth; the two divisions unite again ventrally, probably in segment v, to form the ventral vessel.

The *nephridia* are of the compact type, with a small anteseptal portion and a pear-shaped postseptal; the latter twice as long as the anteseptal, the broad end anterior, the narrow end continued into the duct, which passes downwards and backwards. The duct is about half as long as the postseptal portion, and duct and postseptal together are about twice as long as broad. The first nephridium is in segment v.

The *cerebral ganglion* is large, in segment ii, and has the dorsal vessel closely applied to it underneath. From sections it appears to be slightly convex behind, or at any rate not indented.

Reproductive organs.—The testes are in xi, attached to septum 10/11; there are no sperm-sacs. The funnels are in xi; they are much smaller than is usual in the family, and do not diverge very greatly from the ordinary form; thus there is a small open funnel-like mouth, which is succeeded by a portion of the tube composed of columnar, clear and mucous-looking cells (cf. pl. xii, fig. 6, drawn from a specimen in cedar oil). The vas deferens passes through septum 11/12, is coiled in the anterior part of segment xii, but straight in its posterior portion; it is very narrow, its diameter being 7-8 μ . The penial body, in the posterior part of xii, is spherical, has a diameter of 40-45 μ , and opens on the surface by a wide aperture (pl. xii, fig. 6).

The ovary is attached to septum 11/12. Ova are found in all segments from viii to xii inclusive; segment xii may be largely filled by them (pl. xii, fig. 6). The funnel is a backward depression of septum 12/13 on each side, at its ventral attachment to the body-wall, whence the short narrow oviduct leads directly to the exterior.

The spermathecae open to the exterior in the intersegmental groove 4/5; the ampulla of each is small, approximately spherical or ovoid, in diameter about 30 μ ; it probably communicates with

the oesophagus, though my preparations do not show the actual opening. The duct is several times as long as the ampulla, and is bent once or twice in its course; in diameter it is 11-12 μ .

I may add a few remarks on two of the above characters. The first is the penial body. The Enchytraeidae possess in general glandular structures surrounding the external end of the vas deferens, but differ among themselves in the disposition of the gland-cells; in some cases there are a number of separate aggregates of these cells, opening on the surface of the body around the male aperture, while in other cases the whole of the gland-cells are compacted into a spherical, ovoid, or reniform penial body, surrounding the last part of the vas deferens. Eisen (6) proposes this distinction as a means of separating the Enchytraeidae into two subfamilies, the Lumbricillinae which have, and the Enchytraeinae which have not, a penial body. I have shown however (12) that the representative genera of the subfamilies, *Lumbricillus* and *Enchytracrus*, are connected by a number of forms which have a more or less intermediate position; and that in particular a penial body occurs in more than one species of *Enchytracrus*. It is interesting to find that this is the case in the present species also.

The second point is the condition of the seminal funnel. Its general form in the Enchytraeidae is described by the word 'barrel-shaped,' and this form is occasioned by the excessive elongation of the cells composing the first part of the duct; at the same time the cells become clear and stain only slightly, due presumably to the formation within them of a mucous substance. In the present species the funnel is small, and the change in the cells comparatively slight; the condition is therefore intermediate between that usual in other families and that which is characteristic of the Enchytraeidae.

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